Comparing litter dynamics of *Phragmites australis* and *Spartina alterniflora* in a sub-tropical Chinese estuary: contrasts in early and late decomposition

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Abstract

Litter decomposition in emergent macrophytes can be considered a two-phased decomposition process (standing phase and then a surface one), but little is known about their relative importance. Here, we mimicked this two-phase process and examined the decomposition and nutrient dynamics of three structural components (leaves, flowers, stems) of two common emergent macrophytes in an experimental study in the Min River estuary, southeast China. The two species were *Phragmites australis*, a native species, and *Spartina alterniflora* an invasive one. Decomposition was slower in the standing phase compared to the surface phase for most structural components of both species. In the standing phase, the exponential breakdown rates (*k*-value) for all structural components of *S. alterniflora* were much greater than the corresponding values for *P australis*, whereas, in the surface phase, *S. alterniflora* mostly had lower *k*-values than *P. australis*. The *k*-values in different components of *P. australis* and *S. alterniflora* ranged from 0.00099 to 0.00157 d^{-1} and 0.00193 to 0.00384 d^{-1} in the standing phase respectively and from 0.00272 to 0.00966 d^{-1} and 0.00186 to 0.00879 d^{-1} in the surface phase for the two species respectively. Over the 210 day study, the litter carbon concentrations in three structural components of *P. australis* fluctuated considerably compared to *S. alterniflora*. The variations of nitrogen concentration in flower and stem litter in both species experienced a similar pattern throughout the experimental period, in the surface phase, although the nitrogen concentration increased both in the two species. Litter phosphorus concentration showed a completely different pattern between the two species throughout.

Keywords Aerial position decomposition· surface position decomposition· nitrogen loss· *Spartina alterniflora*· *Phragmites australis*· Min River estuary

Introduction

Decomposition of plant litter and its consequences for litter accumulation are important components of ecosystem function, and as such, it must play a crucial role in the global carbon balance (Tuomi et al. 2009). Decomposition is the process through which organic matter is converted into forms that primary producers can re-use (Park and Cho 2003), and can potentially limit ecosystem productivity. It is, therefore, important to understand nutrient cycling through its complete pathway; from senescence of plant material to decaying plant detritus in the soil.

Wetlands represent the largest component of the terrestrial biological carbon pool (Dixon and Krankina 1995). In spite of this most decomposition studies have been performed in terrestrial systems, where the pre-dominance of aerobic conditions generally results in rapid decomposition of plant debris. In wetlands, however, decomposition occurs at a significantly lower rate, due to anaerobic conditions through the soil profile brought about by flooding at different frequencies and lengths of duration (Debusk and Reddy 2005). Past studies on litter decomposition in wetlands have been mainly focused at the soil surface (Liao et al. 2010; Guo et al. 2008; Song et al. 2011). However, for emergent macrophytes the abscission and collapse of leaf and culms to the sediment surface does not occur immediately after senescence/death, and considerable microbial colonization and subsequent mineralization of standing emergent macrophyte litter may occur before it arrives at the sediment surface (Kuehn and Suberkropp 1998). Little information is available on the relative importance of litter decomposition whilst it remains standing within the vegetation (spring- and early-summer period) relative to when it becomes incorporated into the surface vegetation (autumn- and-winter period) in wetlands.

Litter decomposition rates and associated nutrient dynamics also depend to a large extent on intrinsic chemical properties of the plant detritus input to the litter pool (e.g. carbon (C), nitrogen (N) and phosphorus (P) concentrations) (Enríquez et al. 1993; Lee and Bukaveckas

2002), but environmental factors (temperature, soil moisture content, availability of nutrients) have also been shown to be important (Debusk and Reddy 2005). For estuarine marshes, the frequency and duration of inundation is a key environmental factor as it provides differential conditions of inundation with saline, brackish or fresh water. This frequent inundation will affect the temperature regimes the plants and decomposers experience in both water and air; and hence will affect decomposition in some way. In addition, emergent macrophytes are exposed to differential inundation duration; the lower parts of the stem are submerged for a greater period than the upper parts; and little is known about how decomposition varies with respect to stem height.

Here, we compared the litter decomposition rates and associated nutrient dynamics of six plant parts of two invasive species; a native one *Phragmites australis* Trin, and a recently-introduced one *Spartina alterniflora* Loisel. *P australis* is widely-distributed in fresh-water and brackish coastal wetlands throughout the world. *S. alterniflora* is a native species of brackish and salt marshes of the Atlantic and Gulf Coasts of North America. In 1979, *S. alterniflora* was introduced deliberately to Luoyuan Bay on the Fujian coast, south-east China, in order to provide increased protection of coastal banks, and to accelerate sedimentation and land formation (Liao et al. 2008). Between 2002-2012, however, the rapid spread of *S. alterniflora* has been identified as one of the most damaging impacts on native plant communities in the estuaries of south-east China (Deng et al. 2006). The native *Cyperus malaccensis* Lam. dominated the tidal ecosystem in the middle of the Min River estuary until the 1970s. *P. australis* first colonized the area about 30–40 years ago, presumably by dispersal from stands in the upper section of the estuary, and has since invaded many parts of the marsh formerly dominated by *C. malaccensis*. In 2002, *S. alterniflora* also colonized and is now also displacing *C. malaccensis*. Thus, we have a model system to compare the litter decomposition of two invasive species, a native (*P. australis*) and a recently-introduced one

(*S. alterniflora*).

The aim here was to quantify the natural two-phase decomposition process (standing and surface) in emergent macrophytes. We tested five hypotheses, that decomposition rates would: (1) differ in the standing- and surface-phases, (2) vary between the different plant parts, (3) vary according to their vertical height in the stand during the standing-phase, which might reflect differences in inundation, (4) be affected by resource quality, and (5) vary between the two species.

Methods

The study site was located at the Shanyutan wetland (Longitude, 119°34′12″–119°40′40″; Latitude, 26°00′36″–26°03′42″) on the Min River estuary, southeast China. The estuary has typical semi-diurnal tides, a mean annual temperature of 19.6 ^{o}C, and a mean annual precipitation of 1346 mm. Within this wetland, two adjacent communities (25 m apart) were selected for litter collection and the decomposition experiment: one dominated by *P. australis* and the other by *S. alterniflora*. The height range for both species is typically between 160–180 cm.

Sample collection and preparation

In December 2009, at the end of the growing season when natural senescence would start, standing dead litter of both *P. australis* and *S. alterniflora* were collected to provide the test material for evaluating litter decomposition and nutrient release rates. In the laboratory, these samples were first washed with filtered stream water and then with deionized water to remove sediment and invertebrates, and then separated into different plant structural components (flower, leaf and stem). The stem was further subdivided depending on the length of the standing dead stem, i.e. into 0-30, 30-80, 80-130, 130-180 cm sections; these were then cut into 10 cm long pieces. All material was then air-dried for several weeks and then dried to a constant weight at 70^{o}C to ensure a constant starting material (following Kuehn et al. 1999; Xie et al. 2004; Álvarez and Bécares 2006; Liao et al. 2008; Sun et al. 2012; Song et al. 2011). Litter-bags (25 cm ×30 cm) made of fiberglass 0.3 mm mesh were filled with individual litter components (20 g for leaf and stem and 10 g of flower); 252 bags were produced, i.e. 2 sites/species x 6 components x 7 time samplings x 3 replicates. The litter bags were then returned their respective communities (i.e. *P. australis* litter to the *P. australis* community; *S. alterniflora* litter to the *S. alterniflora* community). The litter bags were retrieved to reflect in

two phases to reflect the standing and dead phases of decomposition as follows:

Phase 1: Standing-phase decomposition. On March 12, 2010, at the start of the growing season, 2 m tall canes were positioned in the centre position within each plant community. Litter-bags were tied to these canes at the positions within the height range of the natural standing dead litter. Litter-bags of each type were retrieved at 0 (no decomposition), 15, 30, 45, 60, 75 and 90 days.

Phase 2: Surface-phase decomposition. On June 12, 2010, mid-way through the growing season, the remaining litter-bags were transferred to random positions on the sediment-litter layer of the marsh. Litter bags of each type were periodically retrieved at 30 day intervals from the wetland, i.e. 120, 150, 180 and 210 days after the start of the experiment.

After retrieval and transfer to the laboratory the litter remaining in all bags was carefully separated, washed and dried as described above. Thereafter, the total carbon (TC), total nitrogen (TN) and total phosphorus (TP) concentrations were determined on each sample. The C and N contents of plants and litter were determined using a Vario EL III Elemental Analyzer (analytical error $\leqslant$0.3%), while P concentrations of all litter samples were determined by molybdate-ascorbic acid colorimetry (digested by H_2SO_4-$HClO_4$), P concentration was measured colorimetrically at 700 nm after reaction with molybdenum blue(analytical error $\leqslant$ 5 %) (Watanabe and Olsen 1965).

Statistical Analysis

Regression analysis (function 'lm', R Development Core Team, 2011) was used to assess the relationship across the entire experiments; here simple linear and second-order polynomial equations were fitted. The proportion of mass remaining at the end of the experiment (p_{210}) and the time for 95% of the starting litter dry mass to decompose were also calculated ($t_{0.95}$) for each plant fraction. Thereafter, for organic matter loss, *k*-values (Olson 1963) were calculated for each phase of the study (k_1=Standing phase (0-90 days; k_2 = Surface phase

(90-210 days) using the simple exponential model (eqn 1) :

$$\log_e(L_t/L_0) = -kt \qquad \text{eqn 1}$$

where L_t is the litter dry mass remaining after t day decomposition, L_0 is the litter dry mass at the start of each phase, K is the decomposition rate or exponential breakdown coefficient and t is the duration (in days) of decomposition. For phase 2, L_0 was set to the mean value of the mass in the 90-day samples (end of Phase 1, start of Phase 2). An analysis of covariance was also performed to test for differences in *k* values (a) between the two phases for each plant part for each species, and (b) between the plant parts of each species over the entire period and in the Standing and Surface phases separately. Here the significant differences in *k*-slopes are reported.

Differences in dry mass remaining, litter nutrient concentrations among plant parts, plant species and the two phases of decomposition were examined by least-significant difference (LSD) approach of ANOVA using the SPSS13.0 (SPSS Inc., Chicago, IL, USA). Thereafter, the relationship between the elemental concentrations through time was assessed using regression analysis; first-, second- and third-order regression equations were fitted (function 'lm') and best-fit equations were fitted to scatter plots.

Results

Dry mass remaining

There were clear differences between species and structural components throughout the experimental period (Fig. 1, Table 1). Over the entire period, decomposition was faster in flowers and leaves compared to stems. For flowers and leaves, the change in dry matter through time were similar in both species (Fig. 1); 25% of flower litter and 22% of leaf litter from *P. australis* remained at the end of the experiment compared to 27% and 16% for S. *alterniflora*, respectively (Table 1). The amount of stem material remaining at the end of the experiment was slighter higher for *P. australis* (range 48-67%) compared to *S. alterniflora (*range 42-55%). The lowest part of the stem for both species had the slowest decomposition rate overall (Table 1).

Decomposition was slower in the standing phase for structural components of *P. australis*, although the flowers and leaves showed a faster rate than the stems, reducing dry matter to 78-80% compared to 87-90% for stems (Table 1). However, for *S. alterniflora* the dry matter loss in all components in the standing phase were significantly greater than for *P. australis* ($F_{1, 10} = 33.86$, $P < 0.01$), 67-72% for flowers and leaves and 68-82% in stems (Table 1).

Litter decomposition rate

These conclusions are borne out by the *k*-values for each species/structural component (Table 2a). In the standing phase, the *k*-value for all structural components of *S. alterniflora* is significantly larger than the corresponding value for *P australis* ($F_{1, 10} = 28.36$, $P < 0.01$). In the standing phase the rank order for *P. australis* was leaves > flower > stem (80-130 cm) > stem (130-180 cm) > stem (30-80 cm) > stem (0-30 cm), whereas for *S. alterniflora* the order changed slightly to stem (0-30 cm) > leaves > stem (30-80 cm) > stem (80-130 cm) > flower > stem (130-180 cm).

In the surface phase, the *k*-values were much greater for the leaves and flowers of *P. australis* compared to the stems, and the rank order of stems was stem (80-130 cm) > stem (30-80 cm) > stem (130-180 cm) > stem (0-30 cm). In this second phase, the leaf and flower components of *S. alterniflora* had lower *k*-values than *P. australis* but they were in the same order of magnitude (Table 2a). K-values for the stems of *S. alterniflora* were largest in the tallest part of the stem (stem (130-180cm) and then reduced with height. Within the stem components, *S. alterniflora* had lower *k*-values in phase 2 than *P. australis*, apart from the 130-180 cm fraction. The *k*-values among plant parts of *S. alterniflora* were not significantly different from that of *P. australis* in the surface phase ($P > 0.05$).

For *P. australis* there were significantly faster decomposition rates in the Surface phase compared to the Standing phase for all plant parts and the stems combined (negative coefficients, all $P < 0.001$, Table 2a). *S. alterniflora*, on the other hand, showed similar responses for stem, leaf and one stem fragment (130-180 cm), but two other stem fragments showed significantly faster rates in the Standing phase (0-30cm and 30-80cm) (positive coefficients, all $P<0.001$, Table 2a). The stem fragments between 80-130 cm showed no significant difference in the two phases.

Results from the analysis of covariance illustrated importance differences between the two phases. Over the entire period there were significant between-species differences only for three of the stem sections (Table 2b) with faster decomposition for *S. alterniflora* compared to *P. australis* (negative slope). However, when decomposition rate in the Standing phase were considered, all plant parts showed significant between-species negative differences in slopes. This indicates that *S. alterniflora* had a faster decomposition rate than *P. australis* (all $P <0.001$, negative Slope coefficient, Table 2b). In the surface phase only two of the stem fragments and the combined stems data showed a significant between-species difference; in all cases the slopes were positive suggesting that these plant parts of *P. australis* decomposed

faster than *S. alterniflora*; there were no significant difference for flowers, leaves or other stem fractions.

Dynamics of litter nutrient concentration

The best-fit relationships between elemental concentration (%) and time are shown in Table 3. During the 210 days decomposing period, the litter C concentrations in the three structural components of *P. australis* all showed a more fluctuating process compared with *S. alterniflora.* C concentrations in flower and stem litter of *P. australis* reached the minimum values at 150 d, and then increased thereafter. The C content decreased to 94 % of the initial value for *P. australis* flower litter after the standing phase, and then it increased to 109 % of initial value of phase 2 after 120 days surface decomposition (Fig. 2). C concentration in leaf litters of *P. australis* was significantly lower than other two components over the whole experimental period ($F_{5, 60}$ = 8.20, P< 0.001). C concentrations in the *S. alterniflora* flower litter demonstrated little variation. However, C concentrations in its leaf litter showed a slow successive increase in the both phases 1. For the stem litter, C concentrations increased in phase 1 and then remained an almost unchangeable process in phase 2. C concentration in leaf litters of *S. alterniflora* was also significantly lower than other two components over whole experimental period（$F_{5, 60}$ = 18.68, P< 0.001). During the decomposition period, C concentration of *S. alterniflora* litter was significantly higher than those of corresponding components of *P. australis*（for all, P < 0.05).

The variations of flower and stem litter N concentration in both species experienced a similar pattern throughout the experimental period (Fig. 3). Flower litter N concentrations all decreased in the standing phase, and then increased in Phase 2. Stem litter N concentrations showed little change during the entire period. The variation in leaf litter N concentration in both species was, however, different. For *P. australis*, the leaf litter N concentration increased over the 210 days decomposition period, although the increase was slower in the standing

phase compared to the surface phase, whereas for *S. alterniflora*, the leaf litter N concentration reduced in the standing phase, then increased during the surface phase (Fig. 3).

By the end of the experiment, the litter N concentration in the three structural components increased to between 112 and 199% of the initial value of phase 2 for *P. australis*, and between 171-234% for *S. alterniflora*, respectively. N concentration in stem litter of *P. australis* was significantly lower than other two components over the whole experimental period（$F_{5,60}$ = 102.59, P< 0.001). N concentration in stem litter of *S. alterniflora* was also lowest in the three components over whole experimental period（$F_{5,60}$ = 35.91, P < 0.001), however there was no significant difference in different sections. We also found the flower litter of *S. alterniflora* had a lower N concentration than that of *P. australis* throughout the experiment ($F_{1, 20}$ = 169.50, P < 0.001).

Litter P concentration showed a completely different change pattern between the two species (Fig. 4). There was a fall in litter P concentration for *P. australis* in the first 15 days, and then an increased in Phase 2. P concentration of *S. alterniflora* was slowly increased at first, and then decreased in the following decomposition phase, at 150 d, the P content fell to its lowest values.

Flower litter P concentration of *P. australis* was significantly greater than that in other two components over the whole experimental period（$F_{5,60}$ = 11.64, P< 0.001). For *S. alterniflora*, flower and leaf litter P concentration were significantly higher than in stems ($F_{5,60}$ = 73.96, P< 0.001). During decomposition, leaf litter P concentration in *S. alterniflora* was significantly greater than that of *P. australis* ($F_{1,20}$ =20.26, P< 0.001, but flower concentration was significantly lower ($F_{1,20}$ = 6.85, P< 0.05).

Over the 210 days, the values of C/N, C/P, N/P in the litters changed at different degrees. C/N in *P. australis* litter showed little change whereas for *S. alterniflora* there was a slow increase in the first 90 d, followed by a marked decline during surface decomposition.

Dynamics of C/P, N/P in the two species differ greatly (Fig. 5). C/P and N/P in *P. australis* rose very quickly after 15 days, and decreased to 60 days but changed little thereafter. C/P in *S. alterniflora* changed little in standing decay period but in Phase 2, C/P of *S. alterniflora* litter increased until 150 d, and then decreased afterwards. C/N, C/P in the flower and leaf litter of both *P. australis* and *S. alterniflora* were significantly lower than stems during the whole decomposition ($P < 0.01$), but N/P in the three structural components was not significant different ($P > 0.05$). C/N in the flower and stem litter of *P. australis* was significantly lower than that in *S. alterniflora* during the decomposition ($P< 0.01$), but C/P and N/P in the leaf litter of *P. australis* were significantly greater than that in *S. alterniflora* ($P < 0.05$).

Discussion

Data on litter decomposition rates show considerable variation in estuarine habitats (Windham et al. 2004). Here, we found that litter of three components (flower, leaf and stem) lost between 33-84% of the initial starting mass after 210 d. Other studies have reported decomposition rates between 20-40% of original dry mass after 46 weeks in three freshwater wetland areas with varying flooding regimes in the Louisiana, US (Conner and Day 1991) and between 40% to 70% loss in the first year within a representative New England salt marsh in US (Valiela et al. 1985). Litter decomposition rate was more slower in a floodplain marsh of the Lower Paraná River, Argentina, remaining 40% to 50% of the initial mass after 2 years incubation (Villar et al. 2001). Our results are at the top end of these ranges, and may reflect a more sub-tropical climate compared to these other study locations. Importantly, however, the decomposition process changed for both species between: (a) the two decomposition phases imposed here; an attempt to mimic the natural processes of decomposition as the material moved for the standing position to the soil surface (Hypothesis 1 accepted), (b) plant

structural part (Hypothesis 2 accepted) and (c) vertical height above the soil surface (Hypothesis 3 accepted). Moreover, decomposition rate was related to the resource quality and specific (Hypothesis 4 and 5 accepted).

At present, there was no a consensus conclusion on whether the invasive species have the same impact on the litter decomposition rate in wetland ecosystems invaded. Invasive *Lythrum salicaria* Linn and native *Typha latifolia* Linn in freshwater marsh in central New York State, had lost similar quantities of litter mass (20-25%) after 1 year (Welsch and Yavitt 2003), however, Vinton and Goergen (2006) found that the invasive *Bromus inermis* Leyss with a lower C/N ratio had a higher decomposition rate than native species *Panicum virgatum* Linn in North America. In the United States, invasive *P. australis* initially decomposed more slowly (37-63% remaining) than those of native *S. alterniflora* (23-53% remaining), but after two years, decay was comparable (8-40% remaining for both species) (Windham et al. 2004). Our results indicated invasive species (*S. alternifolia*) had higher decomposition rates than native species (*P. australis*) in the standing decomposition, no difference in soil surfaces. The higher litter decomposition rate of introduce *S. alternifolia* may be caused by its ecophysiological properties. Liao et al. (2008) found that *S. alternifolia* had a significantly larger net primary production and total litter mass to the standing position than *P. australis*. Additionally, substantial epiphytic N_2 fixation occurred in standing dead shoots of *S. alternifolia*, which attributed to a higher litter quality (i.e. higher N concentration), increased the rate of litter decay. The higher rates of *S. alterniflora* may be one reason for the success of this invasive species.

Standing versus surface decomposition

Decomposition of standing litter in emergent macrophytes of wetland habitats has often been ignored (Newell 1993), but increasingly results suggest that decomposition of the large standing litter present in many wetlands starts in the aerial standing phase (Kuehn et al. 1999).

Valiela et al. (1985), for example, demonstrated a three-phased decomposition process after the litter collapsed to the sediment surface: (1) the early phase lasting less than a month when 5-40% of the litter was lost, (2) a slower phase lasting up to a year when an additional 40-70% may be lost. (3) a very low phase lasting an additional year after which as little as 10% remains. Our study confirmed considerable decomposition weight loss species in the standing phase for both species, i.e. before the material is transferred to the sediment surface. Growing evidence has established that litter is colonized and degraded by fungal assemblages that these microorganisms can contribute to plant litter decomposition before its entry into the aquatic environment (Kuehn and Suberkropp, 1998). Data also provided compelling evidence that microbial decomposition of plant litter occur in the aerial attached-dead phase in most wetlands (Kuehn et al. 2004). Moreover, humidity in the stands of coastal marshlands is high, microbial decomposers that have adapted to the moist conditions can relatively easily colonize the aerial litter (Liao et al. 2008). The decomposition rate in the standing phase was, however, slower than the surface phase for all three structural components (flowers, leaves and stems) tested here for both *P. australis* and *S. alterniflora*. One of the major constraints to decomposition rate is the moisture content and water availability (Sun et al. 2008), and clearly this will regulate microbial activities in the standing phase (Kuehn and Suberkropp 1998), invertebrate might also be lower (Ruppel et al. 2004; Cragg and Bardgett 2001). In this study, tidal water submerged the litter for ten to fifteen times during a month, periodic inundation can speed the decomposition rate of the materials on the sediment surface.

Decomposition rates of the different plant structural parts

The flowers and leaves all showed a faster decomposition rate than the stems for both species and in both the standing and surface decomposition phases. Gessner (2000) studied the breakdown of *P. australis* in a freshwater lake, and found negligible decomposition of culms during the first six months, in contrast, leaves lost 48%; Windham et al. (2004) exposed stems

of *P. australis* decayed somewhat (<20%) and leaves lost about 50% in the first six months. Samiaj and Bärlocher (1996) also found that *S. alterniflora* leaves in a saltmarsh of Canada lost over 60% of their mass in 4 months, which is similar to our findings. The higher initial N concentration (Fig. 3) and lower ratios of the initial C/N (Fig. 5) in flower and leaf than stems may explain the faster decomposition rate. The result is of fundamental importance for nutrient cycling in such estuarine habitats as clearly the decomposition flux of C and other nutrients will be a function of the pool size of each fraction × the decomposition constant for each fraction. C fluxes from the flowers, leaves and stems of *P. australis* were estimated to be 1.43, 1.24 and 0.83 mg g^{-1} d^{-1} respectively and for leaves and stems were lower than comparable rates for *S. alterniflora* (1.40, 1.44, 0.91 mg g^{-1} d^{-1}). For the four stem sections the C fluxes were the litter loss flux of C from the stems was the mean of the litter loss flux of C from the four height strata (surface to top) were 0.59, 0.86, 1.02 and 0.85 mg g^{-1} d^{-1} for *P. australis*, compared to 0.85, 0.84, 0.91 and 1.05 mg g^{-1} d^{-1} for *S. alterniflora*. Irrespective, differences in breakdown patterns of flowers, leaves and stems suggested that they should be studied separately, data on comparable masses of each of the components is needed to develop a whole ecosystem budget.

The role of litter resource quality

Litter quality is commonly defined in terms of the initial C, N, P concentration, C/N, C/P, N/P and lignin/N (Liao et al. 2008). The role of nutrients in the decomposition differed between the two species and they were complex; variations in litter decomposition rates among *S. alternifolia* and *P. australis* can be explained by differences in their litter quality (Berg and McClaugherty 2008). The study of Chimney and Pietro (2006) indicated decomposition rates of the macrophyte litter in a subtropical constructed wetland in south Florida (USA), negative correlations with C/N and C/P ratios, and a positive correlation with N content. In our study, there was a clearly higher initial C/N ratio (31.9-185.1) of litter in introduced *S. alterniflora*

than that of native species *P. australis* (17.2-114.0) during the standing phase ($P<0.01$). However, the decomposition rates of all three structural components of the invasive *S. alterniflora* were faster than the native *P. australis*. The differences may be explained by the dynamics of C/P and N/P. The values of C/P and N/P in *P. australis* litter increased quickly (C/P> 200; N/P> 16) in the first 15 days (Fig. 5). Brinson's suggestion of a C/P ratio of 200 for litter to decompose completely (Brinson 1977), and thresholds of foliar N/P ratios were found to be < 14 for N limitation and > 16 for P limitation (Fenn et al. 1998; Tessier and Raynal 2003). Based on these thresholds it may be inferred that decomposition of *P. australis* litter was limited by P supply. On the other hand, decomposition rates negative correlations with lignin content (Chimney and Pietro, 2006), the higher lignin concentration in the litter of *P. australis* could account for its lower decomposition rates (Liao et al. 2008).

Biomass of *P. australis* litter which was only related to carbon concentration showed little change during the standing phase, but thereafter a rapid decline in the early stages of the surface phase followed by an increase. It is possible that the C losses were due to leaching from the litter on the sediment surface as has been demonstrated for many estuarine macrophytes where considerable amounts of labile DOC can be leached to the water column when submerged (Twilley et al. 1986). The later increase in C concentration may be associated with an increase the proportion of lignin in the remaining litter (Davis III et al. 2003), and lignin is much more recalcitrant than other structural polymers, such as hemicellulose and cellulose(Chimney and Pietro, 2006). The N concentration was also identified as significant for the flower fraction but essentially this element followed the same pattern as the C concentration.

On the other hand, *S. alterniflora* litter biomass was only related to combinations of N and P during decomposition, although there were subtle differences between the two elements. N showed different responses for the three fractions: flowers showed the same pattern as

leaves, declined through the standing phase followed by an increase to above starting values at the end of the process and stems increase throughout. Wrubleski et al. (1997) reported similar initial N responses during decomposition of macrophyte roots/rhizomes through leaching and mass loss and Köchy and Wilson (1997) suggested that nutrient immobilization/ loss depended on the litter quality (C/N and C/P) and nutrient availability in the surrounding environments. The loss of N from litter during early decomposition is likely a result of a higher initial N concentration and a lower initial C/N ratio (Parton et al. 2007), and our study suggested that N start to lost from the litter at C/N ratios of 16.6:1 to 39.9:1 (*P. australis*) and 24.7:1 to 64.3:1 (*S. alterniflora*) as decomposition proceeds, lower than the ratio reported in the forests in Canada (Moore et al. 2006). Microbial communities growing on dead litter surfaces may also contribute to N budgets via atmospheric nitrogen fixation (Moisander et al. 2005) and flooding increased microbial mineralization, may regenerate the immobilized nitrogen in the litter decay (Rice and Tenore 1981).

As the original litters had a large range in C/P ratios, the patterns of P loss or retention are more variable than for N (Moore et al. 2006). In Min River estuary, P concentration showed a fluctuating sinusoidal response for all three fractions with an increase or stasis during the standing phase followed by a decline and subsequent increase towards the end of the process. Twilley et al. (1986）considered that high P leaching from estuarine macrophytes may be related to be a result of the large inorganic fraction of P in tissues. The increased P concentration in the later stages of the decomposition period in the surface phase is a common occurrence and is usually caused by decomposer microbes associated with the plant tissue immobilizing P nutrient for their own growth (Pagioro and Thomaz, 1999; Ozalp et al. 2007). Observed P accumulation in litters was similar to those of Schilling et al. (2006). However, Sun et al. (2012) found that the demand of decomposers was not limited by P supply during the decay in the Sanjiang Plain of China, as a result, superfluous P would retard microbial

activities, causing P to release from the litter at all times, which is different from our study. Underlying mechanisms and issues related to dynamic of P content during the decomposition of litter should be examined in future studies.

Conclusions

The findings obtained in this study strongly support the conclusions that the decay dynamics of wetland emergent macrophytes must include decay processes that occur in the standing dead phase although decomposition rate was slower than on the surface. Our study shows that the mass loss of the invasive species *S. alterniflora* was faster than that of native species *P. australis* in the first 3 months. The result also suggests that the nutrient dynamics is different in the two species litter during the decomposition, decomposition rates depended on the litter quality and nutrient availability in the surrounding environments.

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Table 1 Overall change in dry matter of different structural components of *Phragmites australis* (*P. aus*) and *Spartina alterniflora* (*S.alt*) in the Min River estuary, south-east China – both the standing and surface phases of decomposition are combined. Dry matter was expressed as a proportion of the initial starting mass. Parameters of the regression equations fitted in Fig. 1 are presented. In most cases a second-order polynomial was used, but where the second-order term was not significant a simple linear regression was used. The proportion of the initial mass left at the end the standing phase (P_{90}) and at the end of the surface phase (P_{210}). Significance denoted: * = P<0.05, **= P<0.01, ***= P<0.001.

Species	Coef	Flower	Leaf	Stem 0-30 cm	Stem 30-80 cm	Stem 80-130 cm	Stem 130-180 cm
P. aus	b_0	1.03300***	1.00600***	0.99340***	0.99280***	0.99600***	0.99380***
	b_1	-0.00170**	-0.00153**	-0.00037	-0.00018	-0.00049	-0.00081*
	b_2	-0.00001**	-0.00001***	-0.00001***	-0.00001***	-0.00001***	-0.00001**
	R^2	0.94	0.96	0.96	0.95	0.98	0.96
	P_{d90}	0.80	0.78	0.78	0.90	0.87	0.87
	P_{d210}	0.25	0.22	0.67	0.56	0.48	0.54
S. alt	b_0	1.04406***	1.05514***	0.96120***	0.99690***	0.99596***	1.01600***
	b_1	-0.00356***	-0.00424***	-0.00406***	-0.00321***	-0.00239***	-0.00156***
	b_2			0.00001***	0.000005***		-0.000006**
	R^2	0.94	0.91	0.94	0.96	0.94	0.96
	Pd_{90}	0.72	0.67	0.68	0.75	0.78	0.82
	P_{d210}	0.27	0.16	0.55	0.54	0.49	0.42

Table 2 (a) Decomposition constants (*k*, Olson 1963, i.e. log*e* (Lt/L0) =-*k*t) of different plant parts of *Phragmites australis* (*P. aus*) and *Spartina alterniflora* (*S. alt*) in the Min River estuary, south-east China. Constants for the standing (k_1: 0-90 days)) and surface phases (k_2:90-210 days) of the decomposition process are presented along with an analysis of covariance testing the differences between *k*-slopes for each plant part of each species. The mean value for day 90 was used as the starting value for the calculation of k_2. (b) Results from analysis of covariance testing for differences in *k* between the species (Constant) and responses through time (Slope); this analysis was performed for both periods separately and combined. In these analyses *Phragmites australis* was the intercept. Significance is denoted: ns= P>0.05; **=*P*<0.01, ***=*P*<0.001.

(a)

Species	Plant parts	k_1	k_2	k_1 statistical estimates				k_2 statistical estimates				Analysis of Covariance	
				SE	t	P	Adj R^2	SE	t	P	Adj R^2	Differences between slopes (*k*)	Adj R^2
P.aus	Flower	0.00146	0.00814	0.0003	-5.7180	<0.001***	0.61	0.0004	-20.2380	<0.001***	0.97	-0.00668***	0.98
	Leaf	0.00157	0.00966	0.0002	-8.3990	<0.001***	0.78	0.0005	-17.5830	<0.001***	0.96	-0.00809***	0.98
	Stem(0-30cm)	0.00099	0.00272	0.0001	-11.3200	<0.001***	0.88	0.0003	-8.9190	<0.001***	0.89	-0.00173***	0.95
	Stem(30-80cm)	0.00109	0.00422	0.0001	-14.2170	<0.001***	0.91	0.0004	-10.6000	<0.001***	0.89	-0.00312***	0.94
	Stem(80-130cm)	0.00133	0.00499	0.0002	-8.7870	<0.001***	0.79	0.0003	-15.3350	<0.001***	0.94	-0.00366***	0.97
	Stem(130-180cm)	0.00124	0.00400	0.0001	-11.8780	<0.001***	0.92	0.0004	-8.9160	<0.001***	0.90	-0.00276***	0.96
	Combined stems	0.00114	0.00397	0.00007	-15.4920	<0.001***	0.98	0.0004	-9.8373	<0.001***	0.97	-0.00282***	0.90
S.alt	Flower	0.00237	0.00772	0.0002	-15.0360	<0.001***	0.92	0.0007	-10.9300	<0.001***	0.89	-0.00534***	0.96
	Leaf	0.00330	0.00879	0.0005	-6.7680	<0.001***	0.69	0.0009	-9.5320	<0.001***	0.87	-0.00485***	0.95
	Stem(0-30cm)	0.00384	0.00186	0.0002	-16.0600	<0.001***	0.93	0.0005	-3.9960	<0.01**	0.52	0.00198***	0.91
	Stem(30-80cm)	0.00300	0.00246	0.0002	-12.4170	<0.001***	0.88	0.0003	-8.3720	<0.001***	0.83	0.00054***	0.96
	Stem(80-130cm)	0.00261	0.00301	0.0002	-12.5470	<0.001***	0.89	0.0005	-5.9470	<0.001***	0.74	-0.00041^{ns}	0.93
	Stem(130-180cm)	0.00193	0.00475	0.0003	-7.31000	<0.001***	0.72	0.0003	-13.8800	<0.001***	0.95	-0.00282***	0.97
	Combined stems	0.00288	0.00300	0.0002	-12.5741	<0.001***	0.97	0.0002	-12.8136	<0.001***	0.98	-0.00001^{ns}	0.88

(b)

Plant parts	Combined over both phases		Phase 1:Standing phase		Phase 2: Surface phase	
	Slopes	Adj R^2	Slopes	Adj R^2	Slopes	Adj R^2
Flower	0.00001^{ns}	0.91	-0.00091**	0.83	-0.10215	0.93
Leaf	-0.00146*	0.90	-0.00173**	0.72	-0.50702**	0.92
Stem(0-30cm)	-0.00010***	0.92	-0.00285***	0.96	-0.42595^{ns}	0.87
Stem(30-80cm)	-0.00030^{ns}	0.91	-0.00191***	0.92	-0.42174***	0.90
Stem(80-130cm)	0.000003^{ns}	0.91	-0.001285***	0.89	-0.39474***	0.88
Stem(130-180cm)	-0.000108***	0.91	-0.00070*	0.75	-0.04078^{ns}	0.93
Combined stems	-0.0005608^{ns}	0.87	-0.00168***	0.72	-0.33132***	0.80

Table 3 Regression equations of the relationship between elemental concentration (%) and time for different structural components of *P. australis* and *S. alterniflora* over a 210-day decomposition study in the Min Estuary, south-east China. Relationships were tested up to third-order polynomials and are the equations fitted in Tab. 3; significance coded: ns= no significant relationship (P>0.05) here the overall mean is presented, * = $P<0.05$; ** = $P<0.01$; ***= $P<0.001$.

Elemental	Fraction	*P. australis*					*S. alterniflora*				
		b_0	b_1	b_2	b_3	P	b_0	b_1	b_2	b_3	P
C	Flower	425.73	-7.013	46.062	32.310	0.28**	438.12	-0.043	-	-	0.09*
	Leaf	380.37	18.134	36.209	-	0.18*	400.19	0.143	-	-	0.68***
	Stem	380.37	18.134	36.209	14.206	0.19*	439.07	51.234	-48.409	31.132	0.55**
N	Flower	22.77	-0.348	2.209	8.637	0.34***	8.892	8.961	7.391	-6.990	0.61***
	Leaf	12.60	21.936	7.090	-	0.84***	12.08	10.220	8.891	-	0.74***
	Stem	6.50	9.213	4.125	-	0.26***	4.14	10.23	2.750	-	0.54***
P	Flower	1.29	-	-	-	ns	0.83	0.023	0.673	0.377	0.33***
	Leaf	0.65	1.662	0.753	-	0.54***	1.32	-0.754	0.103	0.840	0.55***
	Stem	0.41	0.759	0.709	-	0.08**	0.34	-0.057	0.1203	0.610	0.39***

Fig. 1. Change in litter mass through time as a proportion of the starting mass for different plant parts of *Phragmites australis* and *Spartina alterniflora* over a 210-day decomposition study in the Min River estuary, south-east China.

Fig. 2. Change in litter carbon concentration ($mg \cdot g^{-1}$) through time for different plant parts of *Phragmites australis* and *Spartina alterniflora* over a 210-day decomposition study in the Min River estuary, south-east China. Parameters for fitted equations are presented in Table 3.

Fig. 3. Change in litter nitrogen concentration ($mg \cdot g^{-1}$) through time for different plant parts of *Phragmites australis* and *Spartina alterniflora* over a 210-day decomposition study in the Min River estuary, south-east China. Parameters for fitted equations are presented in Table 3.

Fig. 4. Change in litter phosphorus concentration ($mg \cdot g^{-1}$) through time for different plant parts of *Phragmites australis* and *Spartina alterniflora* over a 210-day decomposition study in the Min River estuary, south-east China. Parameters for fitted equations are presented in Table 3.

Fig. 5. Changes in litter C:N, C:P and ratios through time for different plant parts of *Phragmites australis* and *Spartina alterniflora* over a 210-day decomposition study in the Min River estuary, south-east China. For clarity mean data are presented, S.E. values were mainly <15% of the mean but are presented in full in Supplementary materials (Table 1-3). Key to plant parts: flowers = open circle, leaves = filled circles, stems (all fractions pooled = filled squares).

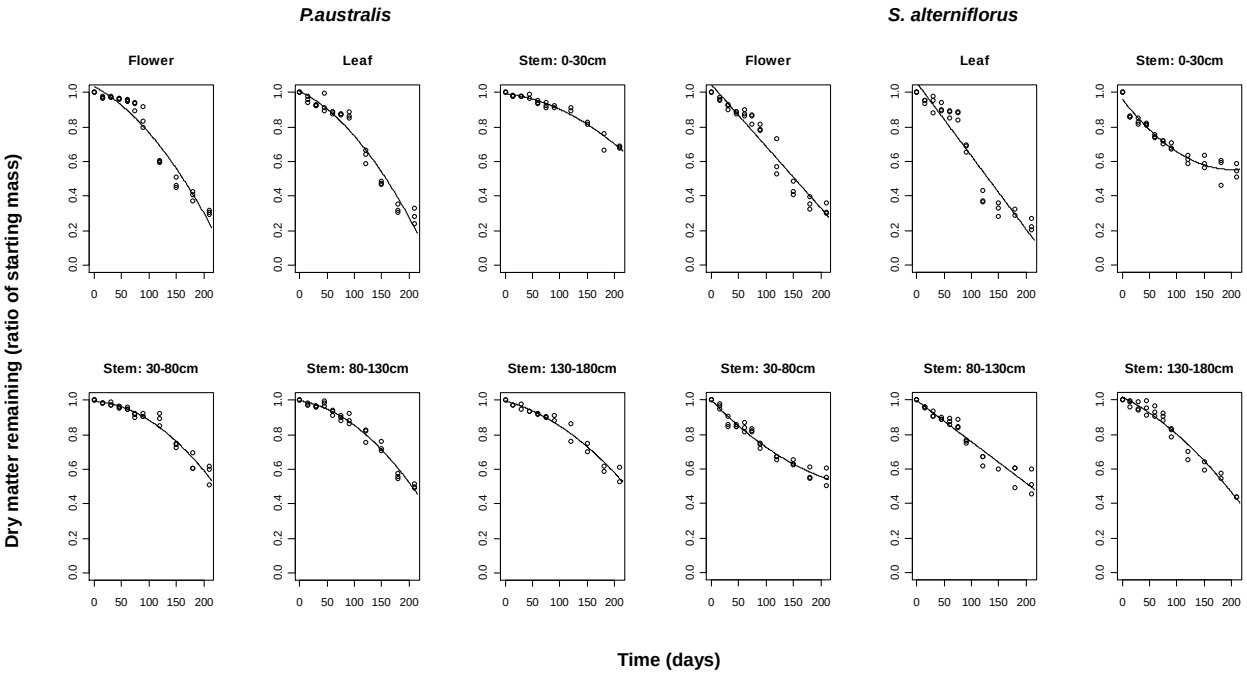
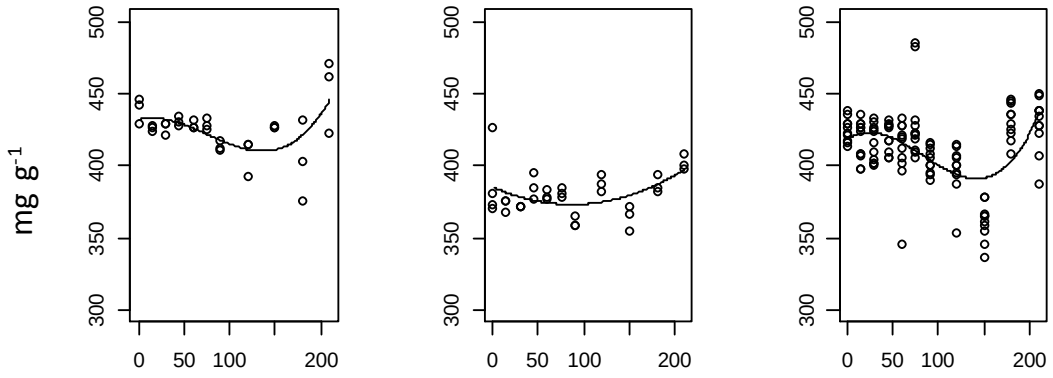


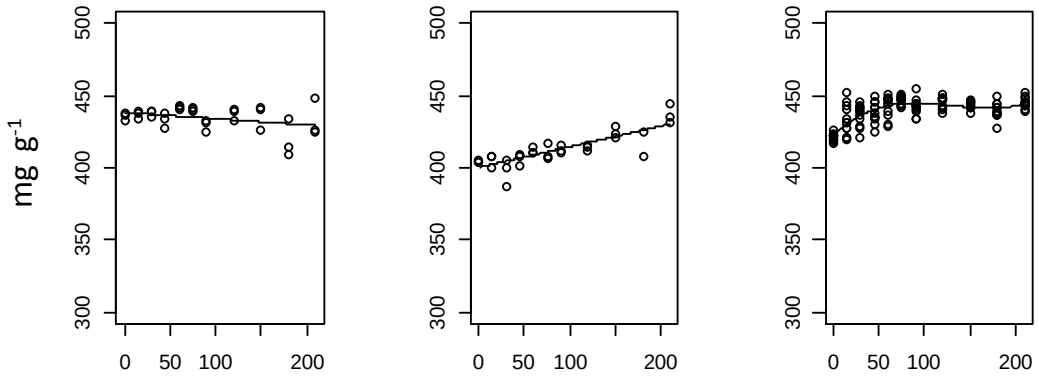
Fig. 1

Leaf Stem

(a) P. australis Flower



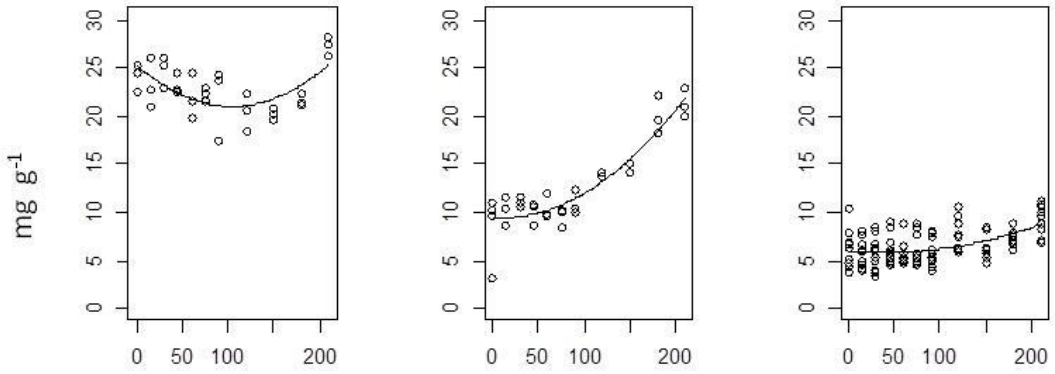
(b) S. alterniflora



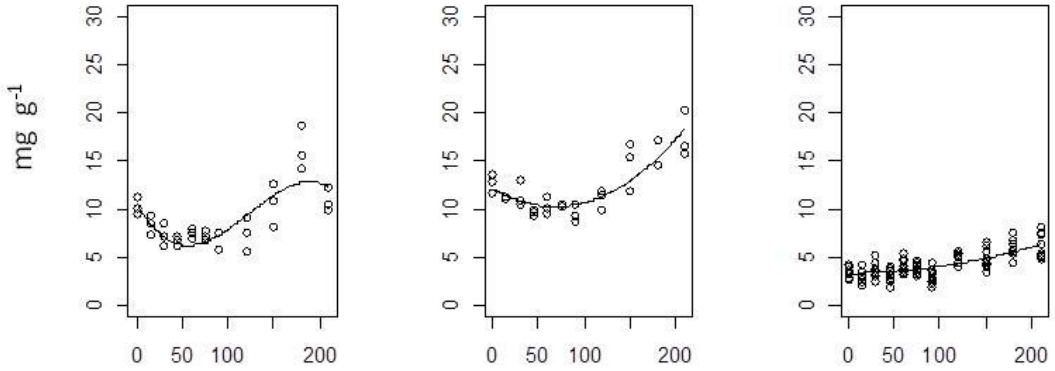
Time (days)

Fig. 2

(a) P. australis Flower Leaf Stem



(b) S. alterniflora



Time (days)

Fig. 3

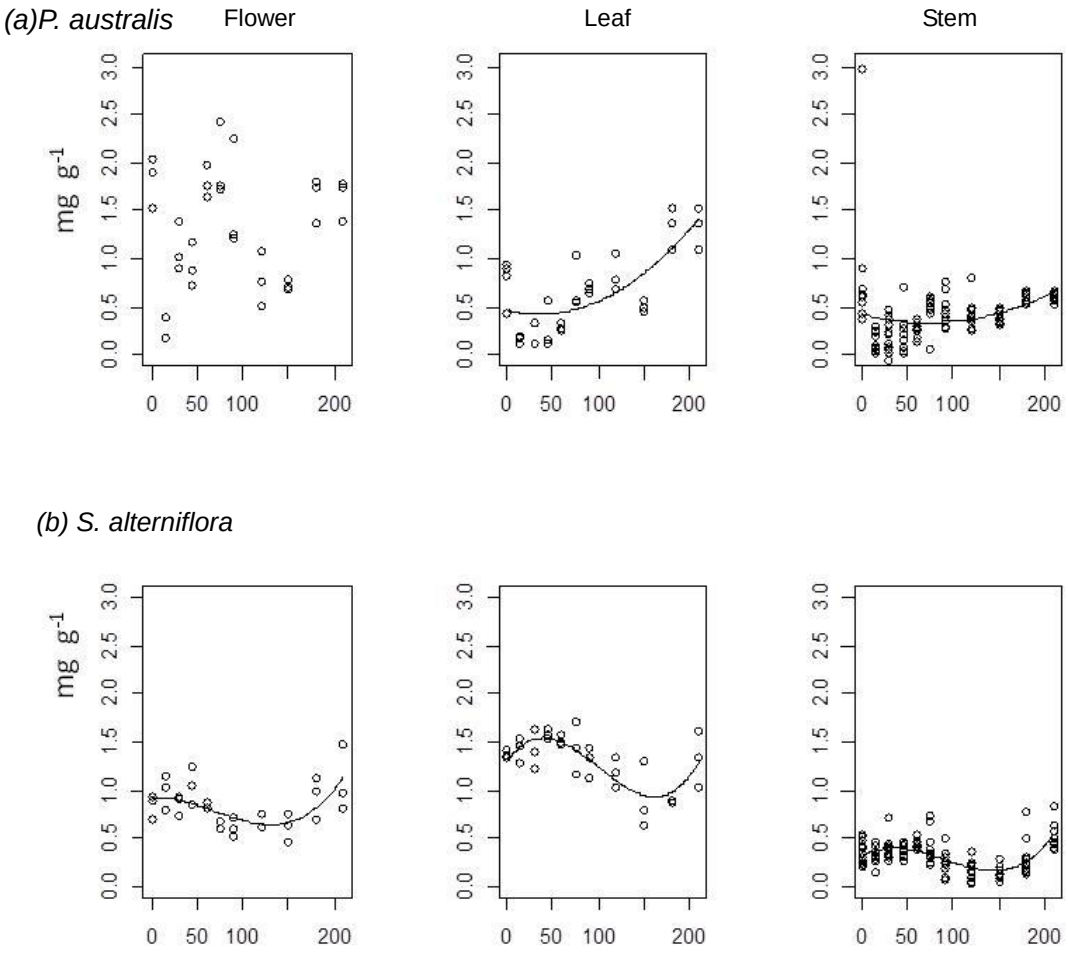
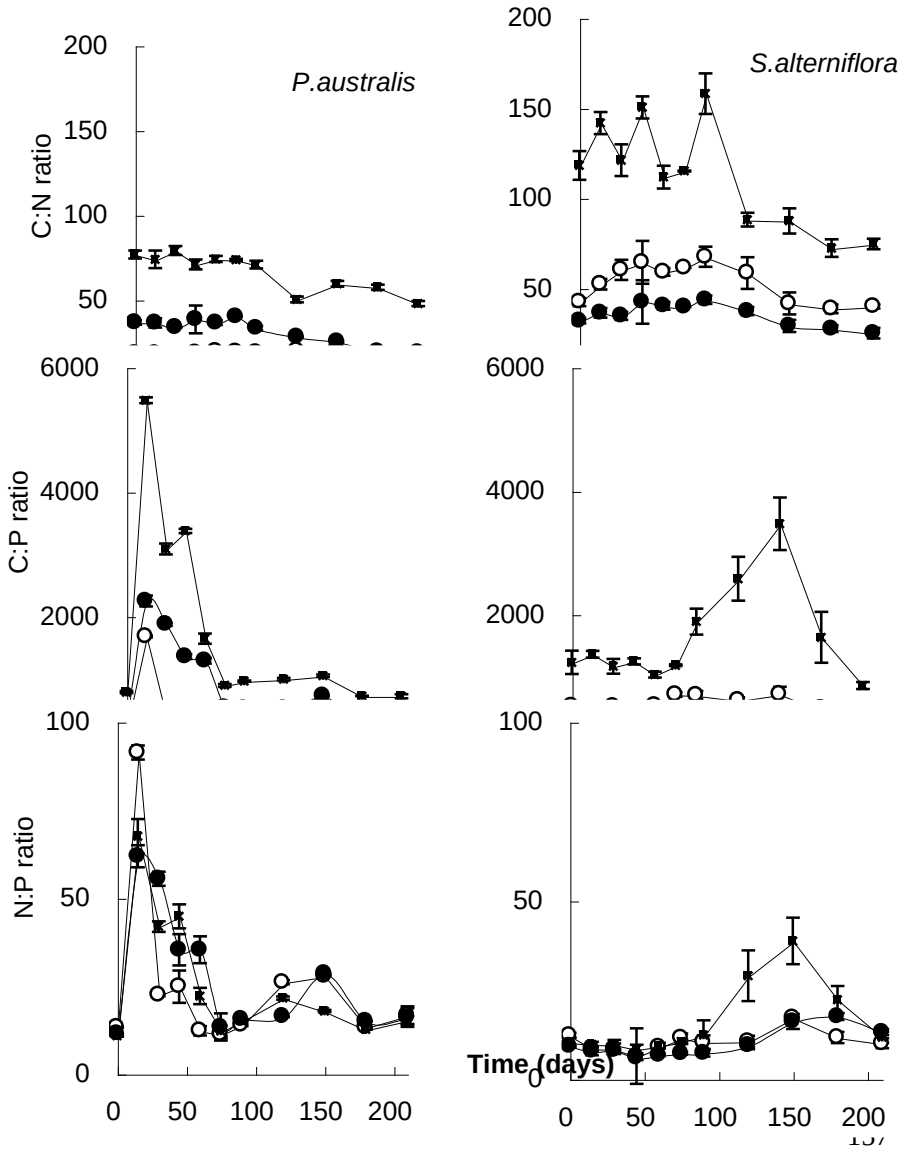

(a)P. australis
Flower
Leaf
Stem
mg g-1
0.0 0.5 1.0 1.5 2.0 2.5 3.0
0 50 100 200
(b) S. alterniflora
mg g-1
0.0 0.5 1.0 1.5 2.0 2.5 3.0
0 50 100 200
Time (days)

Fig. 4


P.australis
S.alterniflora
C:N ratio
C:P ratio
N:P ratio
Time (days)
200
150
100
50
6000
4000
2000
0
0
50
100
150
200